

Continuum model of actin-mediated bacterial propulsion

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The mechanism of propulsion of host bacteria under the action of actin gel networks is examined by means of a continuum model of the dynamics of the F-actin concentration. The model includes the elasticity of the network, its attachment to the host and the polymerization at the interface with it. A formula for the cruise velocity is derived wherefrom the respective contributions of elasticity and polymerization are made explicit. The velocity tends to elongate the gel in the direction opposite to motion, and in turn is proportional to the size of its active portion. It is shown that the motion can start only past a finite latency time: the condition for the onset of motion is explicitly given. It is numerically found that at steady state the motion has a pulsating behavior, with sudden decelerations and subsequent recoveries.

I. INTRODUCTION

The mechanism of actin-induced propulsion has been the object of increasingly sophisticated experiments in recent years [1, 2]. The phenomenon is of interest as a paradigm of more complex situations, and exhibits a variety of fascinating and intriguing features, which keep stimulating new research. In short, an alien host (e.g. a bacterium or a polystyrene sphere) can make the cytoplasmic material to react by polymerizing the resident G-actin into an F-actin gel network surrounding the host's surface; in due time the network evolves into an asymmetric shape, typically comet-like. The host eventually starts moving, and its cruise can last for relatively long times at almost constant velocity. We will focus here on two features of the process; the first one is a threshold mechanism at the onset of motion: the velocity of the host rises from zero to its cruise value quite abruptly, while the mass of the gel undergoes a smooth growth. The second feature is a correlation between the cruise velocity and the length of the comet [1]: longer tails generate higher velocities. This suggests that the dominant role in propulsion stems from a bulk force, rather than from an interface effect, such as the polymerization rate at the host's surface. In fact in cases of growth over convex surfaces it has been observed and proved that the gel elasticity has a primary role: the stress can inhibit the polymerization at the interface [3] and become the main propulsive factor. Disk-shaped hosts can as well be put into motion [4]; one could argue that since the gel coating entirely surrounds the host, the convex portions of its surface are in all cases under the action of stress. It is difficult though to believe that this is an exhaustive explanation when both the cruise velocity and the elongation of the comets are perpendicular to the flat faces of the disks. One must add to the picture the links connecting the gel to the host [5]; such links terminate on the surface at nucleation points, whose distribution is determined by the combined action of various activator groups [6]. The oversimplified digest given above actually translates into a rather intricate dynamical problem, where the global elastic action of the gel, the gel-host links and the polymerization rate come together

into play. This problem is formulated here in terms of a one-dimensional model where the system configuration is described by the gel concentration. The gel velocity is self-consistently determined by generalizing to the time-dependent case the arguments presented in Ref. [7]. The time evolution of the gel concentration is described by a deterministic equation, which includes elasticity and polymerization/depolymerization; the approach being of mean-field type, stochasticity is modeled by a diffusion term. In our formulation the interaction with the host turns into the boundary condition for the concentration: the evolution at the boundary has the form of the tethered ratchet model of Mogilner and Olster [8]. One of the main results of the paper is an explicit formula for the velocity (see below Eq. 7), wherefrom its correlation with the comet size becomes transparent. Furthermore, the origin of the threshold mechanism at the onset of motion is made clear, as a natural outcome of the model. The numerical results shown here exhibit this threshold mechanism as well as an intermittent behavior of the velocity at steady state. The system starts moving past a given "latency" time, which depends on the rate of accretion of the gel, the elasticity and the nucleation rate. The interface polymerization rate can have some relevance in the initial stages after start, but at steady state the bulk contribution prevails: the resulting motion has a pulsating behavior, with sudden reductions of the velocity and consequent recoveries, as in a system alternating "loading" phases at low speed with "unloading" phases at higher speed. (see below Fig. 1).

II. MODEL

As anticipated, we are going to establish a one-dimensional minimal model for the dynamics of the actin gel network during its propulsive action over some host object. We take a macroscopic point of view, where the concentration and the local velocity are a natural choice as dynamical variables describing the gel. Under fairly reasonable assumptions one can get rid of the space dependence of the velocity. The resulting "average" velocity is determined by the concentration: hence the system

is described by this single variable. In turn the average velocity, which we identify with the velocity of the host, appears in the evolution equation for the concentration (see below Eq.6). Let us first show how the host velocity is determined. When the concentration $c(x, t)$ has a well defined peak, say at x_{max} , one can approximate the average of the velocity field $v(x, t)$ as: $\langle v(t) \rangle \approx v(x_{max}, t)$. This obvious remark is not a real progress, unless one relates the unknown quantity $v(x_{max}, t)$ with the value of the velocity field at some other point x_0 where it can in principle be determined: such a point is the contact of the gel with the host [7]. Indeed on the basis of the standard rate theories [9] the velocity at the interface is a function of the elementary work ΔW according with the formula:

$$v_A = v_+ \exp\left(-\frac{\Delta W}{k_B T}\right) - v_- \quad (1)$$

where v_+, v_- are the free polymerization/depolymerization velocities. One has then: $v(x_0, t) = v_A(t)$; the link between $v(x_0, t)$ and the unknown value $v(x_{max}, t)$ is provided by the law of mass conservation. From now on, unless otherwise stated, we are going to use a reference frame comoving with the host, say at velocity v ; the mass conservation reads:

$$\frac{d}{dt}c(x, t) + \frac{d}{dx}[(v(x, t) - v)c(x, t)] = 0. \quad (2)$$

The role of symmetry breaking in the onset of motion is not examined here; let us then assume, e.g., that the gel has grown to the left of the host, so that when the host moves x_0 drifts rightwards. We integrate Eq.2 over the interval $x_b \leq x \leq x_0$, where x_b is a generic position in the gel, and obtain:

$$\int_{x_b}^{x_0} dx \frac{d}{dt}c(x, t) + [v(x_0, t) - v]c(x_0, t) = [v(x_b, t) - v]c(x_b, t) \quad (3)$$

Let us finally assume that the gel and the host drift rigidly together, i.e. that $v \equiv v(t) = v(x_{max}, t)$; upon choosing in Eq. 3 the generic position at the peak of the concentration ($x_b = x_{max}$) we get the relation we were searching for:

$$v(t) = v(x_0, t) + \frac{1}{c(x_0, t)} \int_{x_{max}}^{x_0} dx \frac{d}{dt}c(x, t) \quad (4)$$

This formula gives the velocity $v(t)$ as a nonlocal function of the concentration: the evolution equation for $c(x, t)$ will make our treatment self-consistent. Let us now discuss how such an equation can be determined. The dynamical response of a normal gel, where the structure of the network is fixed by the distribution of crosslinks and of flexible chains, is characterized by well defined values of the coupling constants, such as, e.g., the Young modulus in the case of elasticity. A network of semiflexible, rather than flexible, chains is apparently more apt to describe the actin filaments; whenever its structure is fixed

its elastic response is also defined, but differs from that of a normal gel [10]. Apart from this difference one must be aware of the fact that the actin network of the comets has no predetermined structure: its couplings evolve with the configuration, e.g. the elastic response changes as the mass and crosslink densities build up or decay: it would be appropriate to consider both populations. In the present “minimal” context, where we limit ourselves to the mass density, the compression modulus depends on $c(x, t)$ and the role of crosslinks is included in an effective coupling constant C ; we refer to the Section Elastic Energy for the explicit form of the elastic term.

The environmental factors, such as the “feeding” of polymerization, the depolymerization, the intrinsic fluctuations of the concentration at the microscopic scale, can be assumed to be proportional to the local concentration. Sure enough, the environment evolves with the structure as well, but we will disregard its time evolution for the time being. We consider a potential $U(x)$ (a growth rate), describing the “feeding” and “decaying” processes, in dependence with its sign. Furthermore, a diffusive term accounts for the small scale disorder of the environment, which perturbs a purely deterministic buildup of the network. We add a quadratic term describing the short range self-repulsion between different portions of the structure.

Under such factors, in a static reference frame the concentration would then evolve according to the equation:

$$\frac{d}{dt}c = U(x - vt)c - bc^2 + D \frac{d^2}{dx^2}c \quad (5)$$

where the time dependent potential accounts for the motion of the “activators” which are predominantly concentrated around the host. If, e.g., the potential has a constant value $U > 0$. in the feeding region, its action combined with the repulsive term $-bc^2$ drives $c(x, t)$ towards the value $\bar{c} = U/b$. The host enforces the condition $c(x, t) = 0$. ($x > x_0$); furthermore, the gel is attached to it at the nucleation points and grows against it when the actin filaments polymerize. We model this along the lines proposed by Mogilner and Oster [8], i.e. by means of two concentrations $a(t), w(t)$ respectively describing the “attached” and “working” portions of the gel. Their evolution determines the boundary condition of c at the interface: $c(x_0, t) = a(t) + w(t)$. We now go over and write the evolution equation including the elastic term; this term is proportional to the deviation of the concentration with respect to a reference “background” configuration [11], and is opposite to it. If, e.g., an excess of mass has accumulated in some region during the process of buildup of the network, the elastic force acts as in a spring compressed in the x direction, and elongates the excess of mass along x (see the Section Elastic Energy). The frame comoving with the host has coordinates $x' = x - vt, t' = t$; in these variables the evolution equation has the following form:

$$\frac{d}{dt}c(x, t) = D \frac{d^2}{dx^2}c(x, t) + v \frac{d}{dx}c(x, t)$$

$$+U(x)c(x,t) - bc^2(x,t) - \Gamma \frac{\delta E_{el}}{\delta c(x,t)} \quad (6)$$

where we have dropped the primes; E_{el} is the elastic energy and Γ is the relative decay rate. Notice that a drift term has appeared, in going to the moving frame: it has the effect of elongating the profile of $c(x,t)$ in the direction opposite to v , as if the concentration experienced a backward wind. The higher the velocity, the stronger the effect: the elongation of the profile "measures" the velocity. The velocity and the elongation of the profile actually have a link which goes beyond this purely hydrodynamic effect. In fact, according with Eq.4 the velocity v is in turn c -dependent, and upon inserting the l.h.s. of Eq.6 into Eq.4 we finally get:

$$v = \frac{v(x_0)c(x_0)}{c(x_{max})} + \frac{1}{c(x_{max})} \cdot \left\{ D \left(\frac{dc}{dx} \right)_{x_0} + \int_{x_{max}}^{x_0} dy [U(y)c(y) - bc^2(y) - \Gamma \frac{\delta E_{el}}{\delta c(y)}] \right\} \quad (7)$$

where $x_{max} < x_0$ and the time dependence of the arguments is understood. In the time independent case only the first term survives, and the formula simply states the conservation of stationary fluxes [7]; the boundary term $D(\frac{dc}{dx})_{x_0}$ is negative, as one easily verifies: it averages over the region $x_{max} < x < x_0$ the loss in propulsion originating from network's disorder.

III. NUMERICAL RESULTS

The formula 7 is one of the primary results of the paper; it shows how the velocity gets contributions both from the interface and from the bulk. Notice that v goes as the inverse of the maximal concentration; the elastic force must counter the formation of exceedingly high concentration peaks in order to have higher velocities. The bulk contribution becomes increasingly relevant as the peak at x_{max} moves off x_0 in the backward direction. In the feeding region, close to the interface, we have $U(x) = U > 0$: the network grows and contributes positively to the propulsion. The diffusion constant D ($D = 5 \cdot 10^{-3} (\mu m)^2 / sec$) has a minor effect: its value has been chosen two orders of magnitude smaller than the diffusion constant of monomers within the gel estimated in Ref.[12]. The elastic and self-repulsion terms operate positively or negatively depending on the configuration. They give rise to an intermittent behavior of the velocity even at steady state; typically the velocity 'jumps' between two (or more) values, staying most of the time in one of them, which can be identified with the cruise velocity of the host. Among the temporary, intermittent velocities we found negative values as well: this happens, e.g., when the rate Γ is half the value $\Gamma = 2 \cdot (pN \cdot sec)^{-1} (nm)^{-2}$ used in the simulation presented here. At steady state the motion can be depicted as a sequence of very short "charging" steps, where the

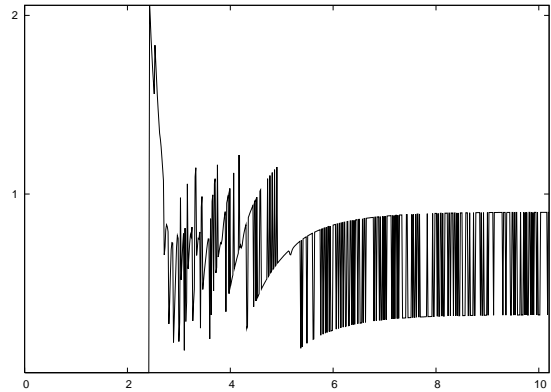


FIG. 1: Typical behavior of the velocity (in units of 10. nm/sec) versus time (in seconds); notice the discontinuity at the onset of motion, the transient before reaching steady state and the intermittent behavior at steady state. The values of the parameters are reported in the text

velocity is small or negative, followed by longer advancement steps. A typical behavior is shown in Fig. 1, where $U = 1 \cdot (sec)^{-1}$: the cruise velocity is $v \approx 8 \cdot nm/sec$, and on average $x_0 - x_{max} = 250 \cdot nm$. The velocity is quite near to $10 \cdot nm/sec$, established in Ref.[1] as a minimum value for classifying an object as being in motion. At a closer inspection the concentration profile reveals time dependent small size deformations tuned with the steps of the velocity. In particular the peak position x_{max} evolves with an intermittent behavior: temporary compressions are subsequently released. Let us call active region the portion of space going from the peak to the interface; in the example shown in Fig.1 this region goes slightly beyond the feeding region, which has size $200 \cdot nm$ (see Fig.3). The formula for the velocity Eq. 7 shows that the bulk contribution is proportional to the size of the active region. A linear relation between the length of the comet and the cruise velocity has been observed in very accurate kinetics experiments by Soo and Theriot [1]: we believe that our results are consistent with such observations. Actually there are two concomitant effects: the drift term elongates the profile by a factor proportional to v , in turn a more elongated profile generates a larger v . Let us examine the interface contribution. According to Eq. 1, $v(x_0)$ is a decaying function of the elementary work ΔW :

$$\begin{aligned} \Delta W &= \delta l \cdot F(x_0) \equiv \delta l \cdot \sigma_{x,x}(x_0) \\ &= \delta l \cdot c(x_0) \frac{a}{w} C_a \int_{x_{max}}^{x_0} dy [c(y) - c(x_0)] \quad (8) \end{aligned}$$

where δl is the elementary displacement having the order of the size of a monomer $\delta l = 2.2 \cdot nm$, $\frac{a}{w}$ the ratio of attached versus working gel and $C_a = 2 \cdot (pN \cdot nm)$ the elastic coupling of the attached portion of the gel. The above expression follows from the equilibrium condition between working forces and load [8], the load here being uniquely given by the attached links (see the Section

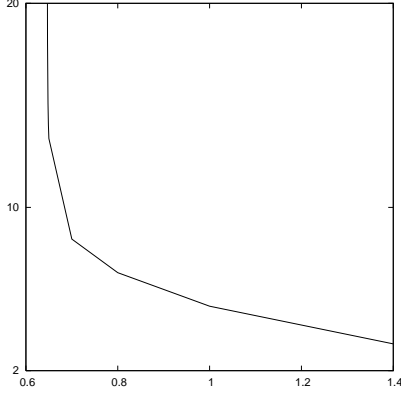


FIG. 2: Latency time (in secs) versus the growth rate U (in units $(\text{sec})^{-1}$); the size of the feeding region is $x_f = 200. \text{ nm}$; notice that when $U < \bar{U} \approx 0.6$ the motion cannot start; these results were obtained with $\Gamma = 0.1 (\text{nm})^{-2} \cdot (\text{pN sec})^{-1}$, $C_a = 1. \text{ pN} \cdot \text{nm}$, $C_w = 0.5 \text{ pN} \cdot \text{nm}$; all the other parameters have values as reported in the text

Elastic Energy). Let us examine the order of magnitude of the force at steady state in the case reported in Fig. 1. There the ratio a/w is close to one (see Fig. 4), the active region has size $x_0 - x_{\text{max}} = 250. \text{ nm}$, the peak is $c(x_{\text{max}}) \approx 10$. (the concentration has units $(10. \text{ nm})^{-1}$) the deviation $c(x_{\text{max}}) - c(x_0)$ is of order 10^{-1} so that one has $F(x_0) \approx 5. \text{ pN}$. Taking into account that the Boltzmann factor is $k_B T \approx 4.1 \text{ pN} \cdot \text{nm}$ one can verify that the contribution to v arising from $v(x_0)$ is quite small as compared with the bulk contribution.

Assuming a free polymerization velocity $v_+ = 10. \text{ nm/sec}$ and $v_- = 0$, we always obtained that the bulk velocity has the dominant role in propulsion, with the exception of the initial transient following the onset of the motion. Our simulations start with zero concentration. A given nucleation rate drives the attached gel ($a(t)$), its decay activates $w(t)$ [8]. As $a(t)$ and $w(t)$ start increasing, the boundary condition $c(x_0, t) = a(t) + w(t)$ initiates the evolution of $c(x, t)$. The velocity does not follow smoothly the gel growth, but rather jumps abruptly from zero to a finite value: the onset of motion has a threshold. The motion can start provided that the gel generates a positive propulsion: this happens when the maximal concentration rises above $c(x_0, t)$: at this point an excess of mass has been created on the back of the host, and the elastic response to it translates into motion. If the gel growth rate is too small, the maximal concentration stays locked at the interface, and the motion cannot start.

If the growth rate is sufficiently high the maximum of c stays at x_0 , but only for a finite “latency” time. This time is strongly dependent on the rate U in the feeding region; in Fig. 2 it is shown that it diverges as U decreases towards a finite value $\bar{U} \approx 0.6$. Similarly, one can verify that shorter feeding regions generate longer latency times. As the peak unlocks from x_0 , the host is instantly put into motion, and its velocity v abruptly departs from

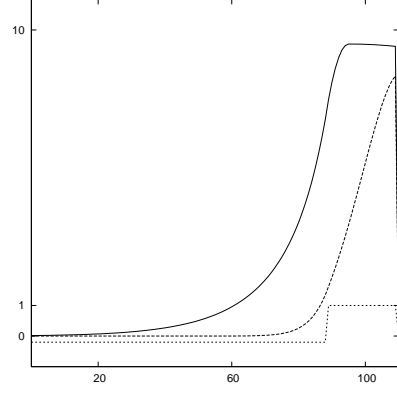


FIG. 3: From bottom to top: potential $U(x)$; profile $c(x)$ at $t=2. \text{ sec}$, right before the onset of motion (dotted line); $c(x)$ at steady state ($t=15. \text{ sec}$) (continuous line). The abscissa has space unit $\bar{a} = 10. \text{ nm}$. The vertical axis is in units $(\text{sec})^{-1}$ ($U(x)$), and $(10. \text{ nm})^{-1}$ ($c(x)$)

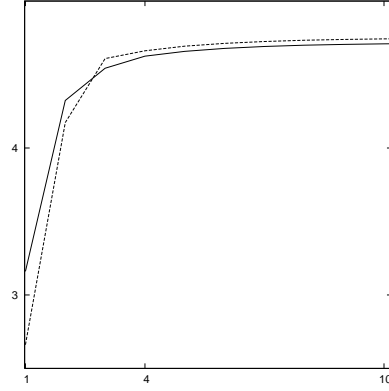


FIG. 4: Time behavior of the variables a (continuous line) and w (dotted line), representing the attached and working part of the gel at the interface; same parameters as in Fig. 1; the vertical axis has units $(10. \text{ nm})^{-1}$, the time unit is $1. \text{ sec}$. At $t=1$, w is still sensibly smaller than a . Notice that at some time $t \approx 2$, w grows above a : this event is close to the onset of motion

zero, with a value depending on the mass accumulated during the latency. In the evolution equation Eq. 6 the drift term is simultaneously activated: the profile is faced with an abrupt backward wind, and must adapt its shape to it. A transient follows, during which the active region modifies its size with strong fluctuations, until the system reaches a steady state profile. In Fig. 3 we compare the profile during latency, but close to start, with the steady state profile; the potential is superimposed [$U(x) = 1$ in the feeding region, $U(x) = -0.2$ in the decay region]. The steady state motion results from the combined action of the drift term and of the elastic forces; the drift term in particular marks the shape of the steady state profile, which appears smoothly elongated away from the interface as compared with its form at the onset of motion. A stationary transfer of mass from the feeding region to

the queue maintains the steady state profile.

IV. ELASTIC ENERGY

We write the elastic energy as a quadratic form

$$E_{el} = \frac{C}{2} \int dx \int dy \delta c(x, t) \cdot G(x, y) \cdot \delta c(y, t) \quad (9)$$

where $\delta c(x, t) = c(x, t) - \bar{c}(x, t)$ is the deviation from a "background" configuration $\bar{c}(x, t)$, C is an energy whose value must account of the effect of crosslinks. The kernel $G(x, y)$ has the role of bounding the range of elastic response within a finite length λ : $G(x, y) = \exp(\frac{-|x-y|}{\lambda})$. We define background or reference configuration a configuration which is in static equilibrium but only over a suitable time scale. New configurations generated at shorter time scales are attracted towards it. In the present paper we give a simplified treatment where the elastic interaction is limited to the active region: we believe that this region has the dominant role in the propulsion. In the bulk of the network the elasticity operates against changes in the concentration profile. The background configuration results from the past hystory of the structure. For the time being we disregard memory effects and simply mimic the rigidity of the system with the self-repulsion term included in Equation 6; the relative coupling constant has value $b = 0.5 \text{ nm/sec}$. Let us focus now on the active region: there a natural choice for the background configuration is given by the concentration at the interface. This is because at the host's surface the concentration is fixed by the boundary condition $c(x_0, t) = a(t) + w(t)$, so that in the adjacent region the profile must be predominantly attracted towards $c(x_0, t)$. In specializing the energy Eq. 9 to the active region we let then $\bar{c}(x, t) = c(x_0, t)$; it is understood that the integrations are extended over the interval $x_{max} < x < x_0$, and we assume $\lambda \gg (x_0 - x_{max})$. About the form of the coupling C , one must consider that the attached and working portions operate in opposite ways and with different strength. The variable $a(t)$ is related with links connecting the gel to the host: their role is of the same nature as that of the gel-gel crosslinks, which determine the bulk's elastic response. Hence $a(t)$ attracts the system towards the background configuration while $w(t)$ acts in the opposite direction. The specific form of the coupling C must then be: $C = \frac{a}{c(x_0)} C_a - \frac{w}{c(x_0)} C_w$ where with C_a and C_w we have separated the elastic response of the attached links from that of the working filaments (we always assume that $C_a > C_w$; in particular in the simulations presented here we have $C_a = 2 \cdot C_w$; $C_w = 1 \cdot pN \cdot nm$). As we assumed that the length λ is much larger than the active region, we average over the space dependence of the deviation: $\delta c(x, t) \approx \delta c \equiv \frac{1}{2}(c(x_{max}, t) - c(x_0, t))$. The total elastic force, proportional to δc , stabilizes the gel provided that the contribution from the gel-host links is the dominant one, i.e. under the condition $C_a \cdot a - C_w \cdot w > 0$.

Let us add some comment on the dynamics of $a(t)$ and $w(t)$: their evolution equations are slightly modified with respect to equations (1) and (2) of Ref. [8]. Here $w(t)$ gets a contribution not only from the detached links, but also from the adjacent gel ($\bar{c} \equiv c(\bar{x})$; $(x_0 - \bar{x}) \ll 1$):

$$\begin{aligned} \dot{a} &= j - \delta(v)a \\ \dot{w} &= \delta(v)a - d_c w + D(\bar{c} - 2w) \end{aligned} \quad (10)$$

here $\delta(v) = \delta_0(1 + \frac{v}{\bar{v}})$ is the velocity-dependent detachment rate, d_c is the capping rate and j is the nucleation rate per space unit. We assigned to these variables the following values: $j = 0.5 \text{ (nm} \cdot \text{sec)}^{-1}$, $\delta_0 = 1 \cdot \text{(sec)}^{-1}$, $\bar{v} = 100 \text{ nm/sec}$, $d_c = 0.8 \text{ (sec)}^{-1}$. It is necessary to connect this formalism with the usual treatment of elasticity: this is done by assuming that the system is incompressible, i.e. that the elementary mass contained in a generic interval Δx is conserved under deformation: $\delta(c(x)\Delta x) = 0$. The condition above gives:

$$\delta c(x) = -c(x) \frac{d}{dx} \Delta x = -c(x) u_{x,x}(x) \quad (11)$$

where $u_{x,x}(x)$ is the strain tensor in one dimension. Eq. 9 then reads:

$$E_{el} = \frac{C}{2} \int dx \int dy [c(x) u_{x,x}(x)] G(x, y) [c(y) u_{y,y}(y)] \quad (12)$$

this should be compared with the standard form of the elastic energy:

$$E_{el} = B \int dx (u_{x,x}(x))^2 \quad (13)$$

The compression modulus B , which in one dimension is an energy/length, in our case is explicitly concentration-dependent. In fact, the stress tensor $\sigma_{x,x}(x)$, which here has the dimension of a force, is given by

$$\begin{aligned} \sigma_{x,x}(x) &= \frac{\delta E_{el}}{\delta u_{x,x}(x)} \\ &= c(x) \frac{\delta E_{el}}{\delta c(x)} \approx C \lambda_{eff} c^2(x) u_{x,x}(x) \end{aligned} \quad (14)$$

where λ_{eff} is the effective range of the interaction. We have then: $B \rightarrow C \lambda_{eff} c^2(x)$. In the case of Fig.3 one would have $B \approx C_a \cdot (x_0 - x_{max}) \cdot c^2(x_{max}) \approx 0.5 \text{ nN}$. Correspondingly the elastic stiffness can be estimated as the ratio $k_{el} = B/(x_0 - x_{max})$: we obtain then $k_{el} = 10^{-3} \text{ nN/nm}$, quite small as compared with the value $k_{el} = 0.17 \text{ nN/nm}$, reported in Ref. [13].

The value of C_a was chosen by requiring a ΔW of order $k_B T$. In the equation of motion the elastic coupling C multiplies Γ , whose value was chosen in order to make the elastic term strong enough to counter an unlimited growth in the feeding region.

From Eq.8 one can argue that a steady state with a ratio $a/w \ll 1$. would allow for higher values of C_a and consequently would give more realistic values of stiffness; the rate Γ should be accordingly reduced, in order to keep the same strength of the elastic term in the equation of motion.

V. CONCLUSIONS

We presented a continuum model of actin-mediated bacterial propagation. The model is a minimal one, in that it describes the system in terms of a single variable: the concentration $c(x, t)$. The time evolution of $c(x, t)$ includes the interaction with the environment and with the host as well as the elastic interaction in the region adjacent to the host's surface. A formula for the velocity is obtained, where the interface and bulk contributions are made explicit. This formula, together with the hydrodynamic effect acting on the profile, makes the correlation between the velocity and the length of the actin network explicit: this result agrees with the behavior observed in Ref. [1], and indicates that the bulk, rather than the interface, has the major role in propulsion. The model furthermore motivates on theoretical grounds the existence of an intrinsic threshold mechanism underlying

the onset of the motion. A relevant feature of a minimal model is that in the numerical simulations the number of adjustable parameters is accordingly quite small. The key parameters regulating the dynamics of the concentration in the bulk are the growth rate U , the self-repulsion coupling b , the elastic coupling C and the rate Γ ; the interface dynamics is controlled by the nucleation, detachment and capping rates (j , $\delta(v)$, d_c). Preliminary numerical results exhibit the threshold mechanism and its dependence on the growth rate (see Figs. 1, 2). The "cruising" steady state is characterized by a pulsating behavior, where the motion undergoes sudden reductions and subsequent recoveries.

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